

## **Pursuit Eye Movements**

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# The Handbook of Brain Theory and Neural Networks

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## **Introduction**

When viewing objects, primates use a combination of saccadic and pursuit eye movements to stabilize the retinal image of the object of regard within the high-acuity region near the fovea. Although these movements involve widespread regions of the nervous system, they mix seamlessly in normal behavior. Saccades are discrete movements that quickly direct the eyes toward a visual target, thereby translating the image of the target from an eccentric retinal location to the fovea. In contrast, pursuit is a continuous movement that slowly rotates the eyes to compensate for the motion of the visual target, minimizing the blur that can compromise visual acuity. While other mammalian species can generate smooth optokinetic eye movements – which track the motion of the entire visual surround – only primates can smoothly pursue a single small element within a complex visual scene, regardless of the motion elsewhere on the retina. This ability likely reflects the greater ability of primates to segment the visual scene, to identify individual visual objects, and to select a target of interest.

residues). For some cases, such methods are comparable to non-network methods which use statistically derived energy functions (Rost and Sander, 1994b).

## Discussion

*Neural networks can be used for predicting structural features of proteins.* There were at least 50 articles on the application of neural networks for protein structure prediction until 1993. One message of the literature is convincing: neural networks can be used to predict secondary structure, structural class, family relations, surface exposure, functional motifs, distance matrices, and even the 3D structure of proteins.

*Neural network methods are seldom superior to non-network approaches.* The second message of the literature is that networks are superior to alternative techniques, but this answer is not convincing! The general problem is a lack of rigor in evaluating results. A common example is the allowance of significant sequence identity between test and training set. Any evaluation that allows for sequence identity has to be compared to homology modeling. And in this comparison, all prediction methods are clearly inferior. The conclusion is that neural network applications have almost never yielded significant improvements over current techniques (Hirst and Sternberg, 1992). An exception is a network that uses evolutionary information to predict secondary structure (Rost and Sander, 1994a). So far, this is the only example for a neural network prediction of protein structure being clearly superior to alternative techniques.

*Neural network predictions have not been made sufficiently available to biochemists.* Unfortunately, the tendency to overestimate the performance accuracy of network prediction has not contributed much to their acceptance by biochemists. Another problem is that almost none of the network methods is publicly available to those researchers who need predictions.

*Neural network techniques will continue to be useful for the prediction of protein structure.* First, the problem of predicting protein structure is far from solved. For a sequence of unknown 3D structure for which no homology to a known fold can be detected, the best one can achieve today is a more or less reliable prediction of secondary structure, surface exposure, or functional class. Second, the constantly growing data banks provide an increasing body of information about protein structure. Chances are that methods based on data bank analysis will be the first to practically solve the prediction of protein 3D structure. Third, neural networks might be well suited for appropriately incorporating the increased information. Using

evolutionary information will be one way to improve predictions by networks. Neural network applications can become increasingly important for the research of tomorrow's molecular biology, provided that testing is done with care and that methods become available to potential users.

**Road Map:** Applications of Neural Networks

**Background:** I.3. Dynamics and Adaptation in Neural Networks

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# Pursuit Eye Movements

Richard J. Krauzlis

## Introduction

When viewing objects, monkeys and humans use a combination of saccadic and pursuit eye movements to keep the retinal image of the object of regard within the high-acuity region near the fovea. While these movements mix seamlessly in normal behavior, their properties and origins are quite distinct. Saccades are ballistic movements that quickly direct the eyes to-

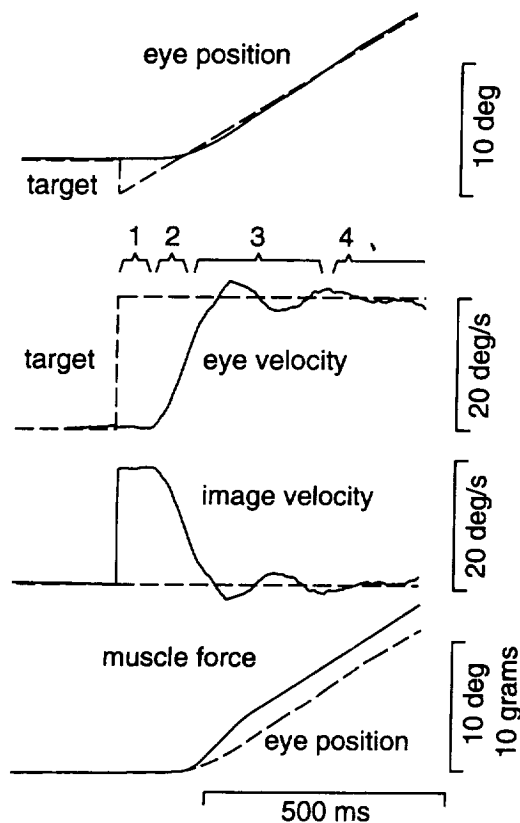
ward a visual target, thereby translating the image of the target from an eccentric retinal location to the fovea. In contrast, pursuit is a continuous movement that slowly rotates the eyes to compensate for any motion of the visual target, minimizing the drift of the target's image across the retina that might otherwise compromise visual acuity. While other mammalian species can generate smooth optokinetic eye movements—which track the motion of the entire visual surround—only primates

can smoothly pursue a single element of a complex visual scene, regardless of the motion this causes elsewhere on the retina. Pursuit eye movements therefore represent a specialization of the primate central nervous system.

### Basic Features of Pursuit Behavior

The basic features of pursuit can be illustrated by considering the *ramp paradigm* (Figure 1), in which a target initially at rest moves at a constant speed. The onset of target motion is often accompanied by a step, eliminating the need for a catch-up saccade (Rashbass, 1961). The eye velocity records obtained with this paradigm can be divided into distinct phases. During the latent phase (1), the target is moving, but the eyes have not yet begun to move. During the initiation of pursuit (2), the eye accelerates at a nearly constant rate related to the image speed experienced during the latent phase. This is followed by a transition phase (3), as eye velocity continues to increase and often overshoots target velocity slightly. During sustained pursuit (4), eye velocity either settles to a steady-state value or oscillates around a value near target velocity.

The ramp paradigm also indicates several of the constraints associated with the pursuit system. First, because the retina is part of the eye, there is a reciprocal relationship between the motion of the target's retinal image and the motion of the eyes. During the latent phase, *image velocity* (the difference between target and eye velocities) is equal to target velocity. After the latent phase, image velocity decreases and then remains near zero during sustained pursuit. Pursuit is therefore organized as



**Figure 1.** Basic features of pursuit can be seen with the ramp paradigm. The target jumps to a slightly eccentric position and moves at a constant speed of 20 degrees per second that is matched by the subject's eye movement after a few hundred milliseconds.

a negative-feedback system: the eye movement output of the system acts to reduce the visual motion input to the system (Robinson, 1981).

Another constraint is imposed by the delay (approximately 100 ms) associated with sensory and motor processing. Combined with negative feedback, this delay could make the system unstable; in fact, under certain conditions, pursuit does exhibit large amplitude oscillations. To compensate for this constraint, the pursuit system uses a combination of short- and long-term predictive mechanisms. For example, it is believed that the motor pathways for pursuit include a circuit that retains the current value of pursuit eye speed. This *velocity integrator* represents a form of short-term prediction and can maintain pursuit eye speed in the absence of vision. Visual inputs (like image velocity in Figure 1) indicate how eye speed should change, and are best related to eye acceleration during pursuit.

Finally, the pursuit system must provide a steadily increasing *muscle force* (Figure 1) to produce a constant-speed eye movement. The required muscle force increases in parallel with eye position as a function of time and can be approximated by taking the mathematical integral of desired eye speed. This process of integration is believed to be common to all eye movements and is accomplished by a *position integrator* contained within the brainstem (Cannon and Robinson, 1987). In addition, the pursuit system compensates for the mechanical aspects of the oculomotor *plant*—the inertial mass of the eye and the visco-elastic properties of the eye muscles. As indicated by the offset between muscle force and eye position, the applied force begins with an additional increment to overcome the sluggish dynamics of the eye (Robinson, 1965). Without this pre-emphasis, it would take three to four times as long for eye speed to match target speed. The neurons innervating the eye muscles during pursuit therefore provide an "inverse dynamics" version of the eye movement command—a signal which, after it is transformed by the eye plant, produces the desired eye motion.

### Models of Pursuit

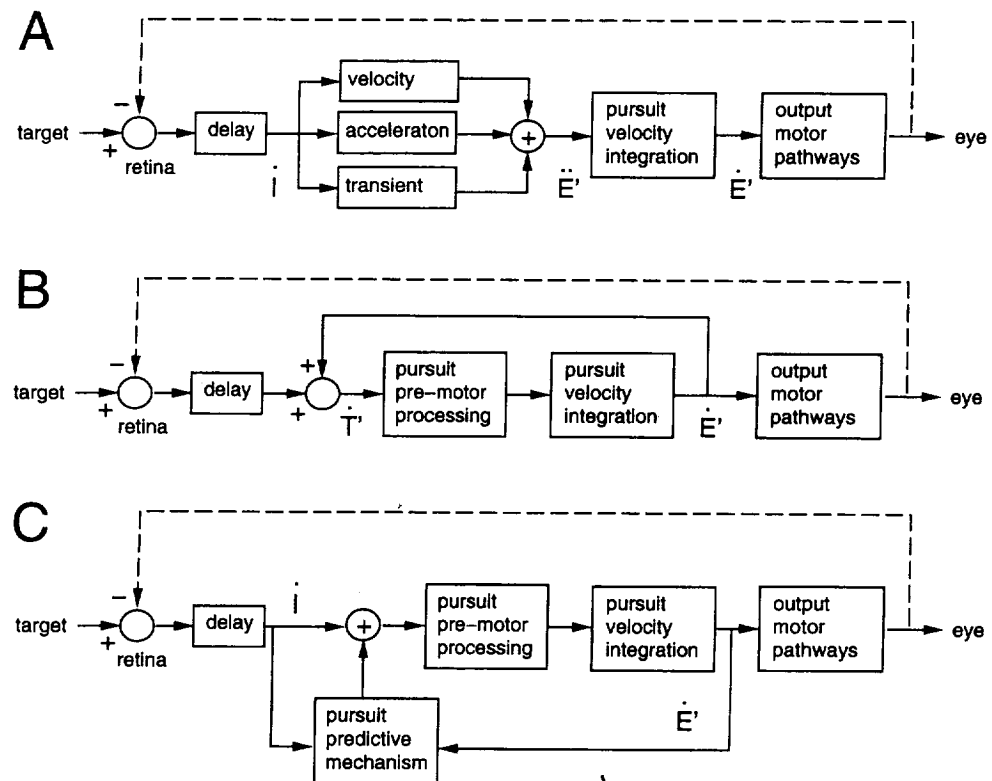
Current models of pursuit vary in their organization and in the features of pursuit that they are designed to reproduce. However, they are similar in that they are concerned with describing pursuit behavior without explicit reference to the neural structures that might be responsible.

*Image motion* models (Figure 2A) focus on replicating in detail the initial increase in eye velocity at the initiation of pursuit, the overshoot in eye velocity during the transition to sustained pursuit, and the oscillations observed during sustained pursuit (Krauzlis and Lisberger, 1989). The key feature of these models is the presence of multiple visual inputs, which are designed to reflect the complexity of the visual signals used to drive pursuit. In these models, the temporal features of pursuit eye movements (see Figure 1) are matched primarily by adjusting the dynamics of the visual inputs, while the premotor processing is simplified.

*Target velocity* models (Figure 2B) also can replicate the profile of eye velocity as a subject initiates and maintains pursuit, but they use a different structure (Robinson, Gordon, and Gordon, 1986). The key feature of these models is the construction of an estimate of target motion by adding a copy of the eye velocity output to the visual motion input. In these models, the processing of visual inputs is greatly simplified, and the characteristic features of pursuit are accomplished by the properties of the premotor processing.

Despite the differences between these two classes of models, they accomplish similar transformations of the input signal

**Figure 2.** Three classes of pursuit models. The input to each model is target speed; the output is eye speed. The dashed lines indicate the physical coupling of the eye and retina. *A*, *Image motion* models include complex processing of visual motion inputs for pursuit. *B*, In *target velocity* models, a positive-feedback loop is used to construct an internal estimate of target velocity. *C*, In *predictive* models, the output from a long-range predictive mechanism provides an additional input for pursuit.



**Table 1.** Summary of Physiological Studies of Pursuit

Structure	A. Lesions	B. Electrical Stimulation	C. Single-Unit Recording
1. V1	Deficits in saccades and pursuit		
2. Extrafoveal MT	Transient retinotopic deficits in the initiation of pursuit		Visual responses tuned for direction/speed of small stimuli
3. Foveal MT	Deficits in initiating pursuit; deficits for ipsilateral sustained pursuit	Ipsilateral eye acceleration if applied during sustained pursuit	Visual responses to motion of small stimuli
4. MST	Deficits in initiating pursuit; deficits for ipsilateral sustained pursuit	Ipsilateral eye acceleration if applied during sustained pursuit	Visual responses to motion of small or large stimuli; nonvisual responses
5. 7a, VIP			Visual responses to stimulus motion; nonvisual responses
6. FEF	Deficits in sustained and predictive or anticipatory pursuit	Eye acceleration, often ipsilateral, if applied during fixation or pursuit	Visual responses to stimulus motion responses during tracking
7. DLPN	Deficits in initiating pursuit; deficits for ipsilateral sustained pursuit	Ipsilateral eye acceleration if applied during sustained pursuit	Visual responses best for moving large stimuli; nonvisual responses
8. DMPN, NRTP	Deficits in pursuit		Visual responses to large stimuli
9. NOT	Deficits in ipsilateral tracking	Ipsilateral eye acceleration	Visual responses to large stimuli
10. LTN			Visual responses to large stimuli
11. Ventral paraflocculus	Long-lasting deficit in pursuit	Ipsilateral eye acceleration if applied during fixation or pursuit	Responses to eye and head velocity; visual responses during pursuit
12. Oculomotor vermis	Long-lasting deficit in pursuit	Evokes saccadic eye movements	Responses to eye and head velocity, passive visual responses
13. VN, FN, NPH	Sustained deficits in pursuit and saccadic eye movements		

Details of experimental findings can be found in several longer reviews (Eckmiller, 1987; Keller and Heinen, 1991; Krauzlis, 1994; Lisberger, Morris, and Tychsen, 1987).

and, with certain simplifying assumptions, can be shown to be formally equivalent (Deno, Keller, and Crandall, 1989). However, structural differences between the models do have implications. For example, it has been observed that image motion models can account for the altered pursuit found when the delay in the visual feedback is changed, while target velocity models cannot (Goldreich, Krauzlis, and Lisberger, 1992).

*Predictive models* (Figure 2C) address the role of prediction in pursuit. These models cover a wide range of approaches, but they share the feature of asserting that mechanisms other than immediate processing of visual inputs are required to replicate all features of pursuit behavior (Barnes, 1993). These mechanisms often involve extracting and subsequently recognizing patterns of target motion. This additional information can supersede the effects of visual feedback and produce movements that are not simply visual reflexes.

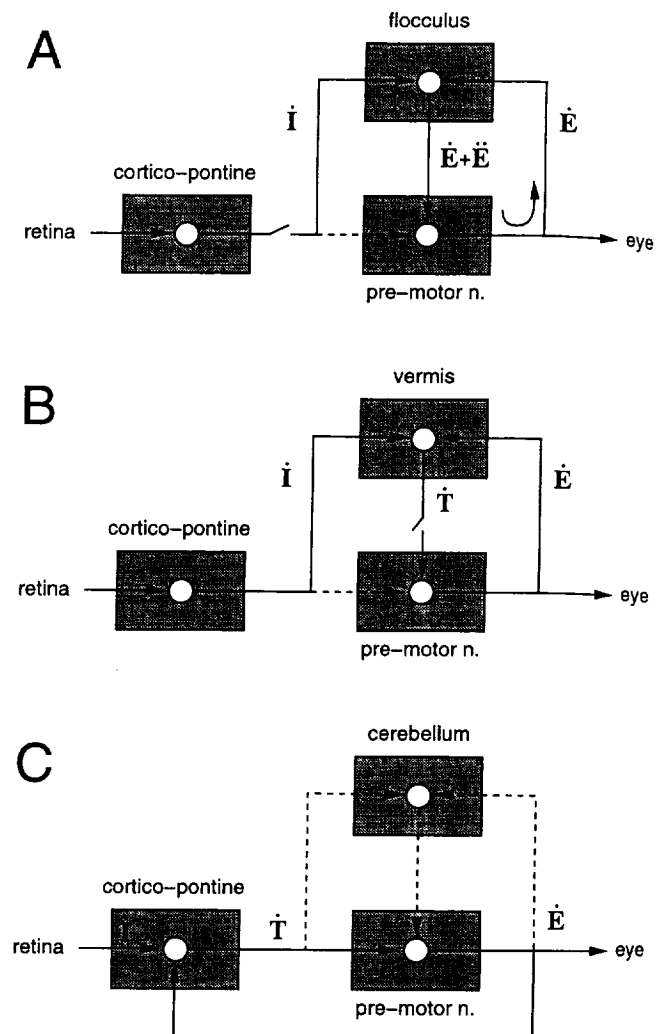
### The Neural Pathways for Pursuit

The importance of both visual areas of the cerebral cortex and oculomotor regions of the cerebellum have been clearly demonstrated by experimental lesions (Table 1). These results suggest that the cerebral cortex provides sensory inputs that the cerebellum and premotor nuclei, in turn, convert into commands for pursuit. However, several observations argue that the conveyance of activity along the cortico-ponto-cerebellar pathways does not constitute a straightforward progression of visual signals toward commands for pursuit. For example, some of the signals provided by the cerebral cortex are not purely visual. Nonvisual signals have been demonstrated by recording the activity of isolated units as a monkey continuously tracks a target moving in the units' preferred direction. When the target is briefly turned off, the response of neurons in several regions continues unabated. Conversely, visual signals have been recorded at the level of the cerebellum, in addition to "motor" signals related to eye movements. Furthermore, electrical stimulation of some sites produces pursuitlike movements only if the subject is already engaged in pursuit, while stimulation of other sites produces smooth movements whether the subject is pursuing or fixating. These effects suggest that the pursuit pathways contain a "switch" that governs the transmission of sensory and motor signals, an idea consistent with the behavioral distinctions that can be drawn between pursuit and other eye movements (Luebke and Robinson, 1988).

### Perspectives on the Neural Pathways for Pursuit

To illustrate the difficulties in drawing conclusions about the overall organization of the neural pathways for pursuit, we next consider how three particular structures—the floccular region, the oculomotor vermis, and extrastriate cortex—may contribute to pursuit.

During sustained pursuit, floccular Purkinje cells (the cerebellar output neurons) show a continuous increase or decrease in firing rate. This sustained activity is suggested to result from the reciprocal connections between the floccular region and the premotor nuclei (Figure 3A). The loop formed by these connections could provide the neural substrate for the pursuit velocity integrator included in the pursuit models (see Figure 2). Furthermore, these Purkinje cells display transient responses to moving stimuli that are the object of a pursuit eye movement, but only modest responses to stimuli presented during fixation. These transient responses at the initiation of pursuit may reflect visual inputs to the floccular region that drive the initial acceleration of the eye ( $\ddot{E}$ ) and are then incorporated through feedback into the sustained eye velocity command ( $\dot{E}$ ), analogous



**Figure 3.** Three perspectives on the neural substrates for pursuit. *A*, The output of the floccular region may represent a command for pursuit eye velocity ( $\dot{E}$ ) and eye acceleration ( $\ddot{E}$ ). The broken line at the output of the corticopontine pathways indicates that the pursuit "switch" appears to lie upstream. *B*, The output of the vermis may represent a neural reconstruction of target velocity. The pursuit "switch" appears to lie downstream of the vermis. *C*, The output of the corticopontine pathways may provide a signal that already encodes target velocity and can be used directly by the premotor nuclei for pursuit.

to the flow of signals in the image motion models (see Figure 2A). Another similarity is that this scheme does not include an internal estimate of target motion.

Like the floccular region, the oculomotor vermis receives a combination of visual and eye motion inputs (Figure 3B). However, vermal Purkinje cells respond to moving stimuli presented during fixation or pursuit. This conditional linkage between activity in the vermis and pursuit eye movements, indicated by the "switch" in Figure 3B, suggests that the vermis may be part of a premotor circuit that provides a set of candidate signals for pursuit. As in the target velocity models (see Figure 2B), the combination of visual and eye motion signals may be used to construct an internal estimate of target motion.

In extrastriate cortex, there are several sites where eye movement signals have been found in conjunction with visual mo-

tion signals, such as the medial superior temporal area (MST), the frontal eye fields (FEF), and the posterior parietal cortex. Ablation of these areas leads to deficits in both initiating and sustaining pursuit. These results suggest that cortical inputs may be sufficient to drive pursuit and that the critical neural pathway may be a direct link between the cerebral cortex and the brainstem (Figure 3C). If the critical computations for pursuit were accomplished in the cerebral cortex, the pursuit deficits resulting from cerebellar lesions might be viewed as one aspect of a general deficit in oculomotor control. For example, the cerebellum might be important for compensating for the mechanical properties of the eye plant, a function associated with the output motor pathways in the pursuit models (see Figure 2), while the cerebral cortex might compute the internal estimates of target motion that are used to drive pursuit, a function associated with the predictive or premotor elements in the pursuit models.

### Discussion

The aim of this article has been to draw parallels between behavioral, modeling, and physiological approaches to the study of pursuit. The current challenge is to bridge the gap between mathematical models and physiological data. Toward this end, models of pursuit need to become more biomorphic; their organization needs to conform more closely to known anatomy, and their components need to resemble more nearly actual neurons. Conversely, physiological studies of pursuit should explicitly recognize the conceptual models underlying their design and produce quantitative tests of those models.

**Road Map:** Primate Motor Control

**Background:** Motor Control, Biological and Theoretical

**Related Reading:** Cerebellum and Motor Control; Collicular Visuomotor Transformations for Saccades

## Radial Basis Function Networks

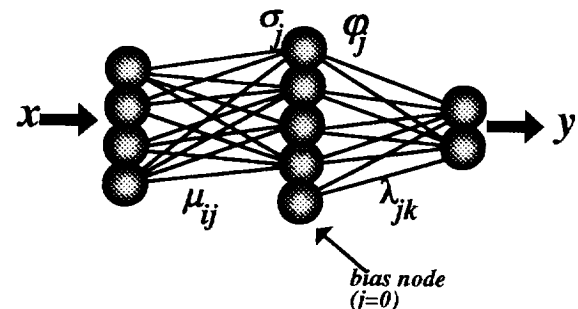
David Lowe

### Introduction

The Radial Basis Function Network (RBFN) is conceptually a very simple and yet intrinsically powerful network structure. The radial basis function network constructs global approximations to functions using combinations of "basis" functions "centered" around weight vectors (Figure 1), whereas a multi-layer perceptron constructs an architecture out of separating hyperplanes. An extra distinction is that the radial basis function employs a distance function to convert the vector input pattern into a scalar at the hidden layer, as opposed to a vector dot product. The network's strength derives from a rich interpretational foundation, since it lies at the confluence of a variety of "established" scientific disciplines. Thus, although the original motivation of this particular network structure was in terms of functional approximation techniques, the network may be "derived" on the basis of statistical pattern processing theory, regression and regularization, biological pattern formation, mapping in the presence of noisy data, and so on. However, in addition to exhibiting a range of useful theoretical properties, it is above all a practically useful construct as it

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**Figure 1.** The basic radial basis function structure. There is a nonlinear basis function  $\phi_j(\dots)$  centered around each hidden node weight vector  $\mu$  which also has a (possibly) adaptable "range of influence"  $\sigma_j$ . The output of the hidden node  $j$ ,  $h_j$  is given as a radial function of the distance between each pattern vector and each hidden node weight vector,  $h_j = \phi_j(\|x - \mu_j\|/\sigma_j)$ . This is the main difference from a multi-layer perceptron. The network outputs are evaluated by a traditional scalar product between the vector of hidden node outputs and the weight vector attached to output node  $k$ , as  $o_k = h \cdot \lambda_k$ .